

# Fascicle nutrient and biomass responses of young loblolly pine to control of woody and herbaceous competitors

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**Abstract:** Individual fascicle mass and foliar nutrient content and concentration of young loblolly pine (*Pinus taeda* L.) were evaluated on 13 locations of a regionwide competition study in the southeastern United States. The study included a factorial combination of two levels of herbaceous weed control treatment (none, treated) and two levels of woody treatment (none, treated) following site preparation. At pine age 2 years, herbaceous treatment (HT) and woody treatment (WT) had a positive effect on individual fascicle biomass and content of N, P, and K at nearly all and at least half of the locations, respectively. In general, these effects mirrored responses noted for seedling diameter and height. N concentration increased and P concentration decreased at about half of the locations, while Ca and Mg concentrations decreased on nearly all locations with HT. By age 6 years, effects of HT and WT on fascicle mass and nutrient concentrations and contents became neutral or more neutral across the locations. This is attributed in part to the greater nutrient demand of larger crop pines and associated competition components. A notable exception from neutral effects at age 6, typically occurring on sites with high levels of woody vegetation, was the positive response in K concentration or content and negative response in Ca and Mg concentrations with WT.

**Résumé :** La masse des fascicules individuels, de même que le contenu et la concentration foliaire en éléments nutritifs de jeunes pins à encens (*Pinus taeda* L.) ont été étudiés à 13 endroits faisant partie d'une étude régionale de compétition dans le sud-est des États-Unis. L'étude inclut une combinaison factorielle de deux niveaux de répression de la végétation herbacée (aucun, traité) et deux traitements de la végétation ligneuse (aucun, traité), appliqués après une préparation de terrain. Pour des pins de 2 ans, le traitement des herbacées et le traitement des essences ligneuses ont eu un effet positif sur la biomasse des fascicules individuels sur presque toutes les stations, de même que sur le contenu en N, P et K sur au moins la moitié des stations. En général, ces effets reflétaient les réactions des semis en diamètre et en hauteur. La concentration en N a augmenté et celle de P a diminué sur environ la moitié des stations, tandis que les concentrations en Ca et Mg ont diminué sur presque toutes les stations où un traitement de la végétation herbacée avait été appliqué. À 6 ans, l'effet des traitements sur la masse des fascicules de même que sur le contenu et la concentration en éléments nutritifs est devenu neutre ou plus neutre pour l'ensemble des stations. Ceci est attribué en partie à une plus grande demande en éléments nutritifs liée à la plus grande taille des pins et à la végétation compétitrice. La réaction positive des concentrations et des contenus en K et la réaction négative des concentrations en Ca et Mg suite à la répression de la végétation ligneuse constituent une exception notable à la neutralité des effets à 6 ans, qui survient typiquement sur des stations avec une forte végétation ligneuse.

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## Introduction

Woody and herbaceous weeds have been shown to have a significant negative impact on survival and (or) growth of planted loblolly pine (*Pinus taeda* L.) in the southeastern United States (Nelson et al. 1981; Zutter et al. 1986a, 1986b;

Bacon and Zedaker 1987; Miller et al. 1987, 1991). Most research studies have focused on the effects of controlling only herbaceous vegetation (e.g., Nelson et al. 1981; Creighton et al. 1987; Lauer et al. 1993), only woody vegetation

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(e.g., Langdon and Trousdell 1974; De Wit and Terry 1982; Glover et al. 1991), or controlling both components (e.g., Swindell et al. 1988). As a result, our understanding of how woody and herbaceous plants may interact to influence the growth and development of loblolly pine is limited (Bacon and Zedaker 1987). In the early 1980s the Competition Omission Monitoring Project (COMP) was developed, in part, to compare the relative effects of woody and herbaceous plants and their interaction on the response of loblolly pine across a wide range of sites in the southeastern United States.

Although there is an abundance of information relating loblolly pine response to the amount of competing herbaceous and (or) woody plants, the underlying causes or mechanisms for such responses are less well understood. A number of studies have shown soil water to increase and water stress of loblolly pine seedlings to be lessened in the absence of woody and (or) herbaceous vegetation (Nelson et al. 1981; Miller et al. 1987; Byrne et al. 1987; Perry et al. 1994). Light availability to loblolly pine seedlings has been shown to be inversely related to the amount of competing vegetation (Nusser and Wentworth 1987; Morris et al. 1993; Mitchell et al. 1998). However, little is understood with regard to the effects of woody and (or) herbaceous plants on soil nutrient availability (Allen and Wentworth 1993) and nutritional status of loblolly pine seedlings and how the nutritional status may change with seedling growth and development. Since disturbances associated with harvesting and site preparation increase the availability of nutrients (Jokela et al. 1991), suppression of reestablishing woody and (or) herbaceous vegetation following planting could dramatically increase nutrient availability to loblolly pine seedlings. It is unclear whether seedling response would be observed in increases in individual fascicle nutrient content and (or) concentration in addition to increases in individual fascicle mass and total foliage biomass noted by Zutter et al. (1986b). Increases in foliar nutrient concentration in one year could provide an additional source of nutrients for development of foliage the following year and contribute to rapid crown development.

The objective of this study was to determine foliar nutrient responses of young loblolly pine 2 and 6 years after planting under conditions of no additional control, herbaceous control only, woody control only, and herbaceous and woody control following site preparation on COMP study sites across the southeastern United States. The use of a standard experimental protocol and the wide range in soils (and associated site quality), physiographic provinces, geographic distribution, and levels of woody vegetation among study locations allows for a more comprehensive look at nutrient responses than that from a single location or examination of several independent experiments.

## Materials and methods

Study locations of COMP are distributed across several physiographic provinces from Louisiana to Georgia and Tennessee to Virginia (Table 1). In general, most sites were previously occupied by loblolly pine – hardwood or mixed loblolly pine – shortleaf pine (*Pinus echinata* Mill.) – hardwood stands. Following a commercial timber harvest the sites were typically roller-drum chopped and burned and then planted in January or February. Commercial 1-0

bareroot seedlings were hand planted at a spacing of  $2.74 \times 2.74$  m (1329 trees/ha) on most study sites. Seedlings were machine planted at Pembroke ( $2.13 \times 3.35$  m, 1397 trees/ha) and Arcadia ( $2.13 \times 3.05$  m, 1537 trees/ha). Mean density 1 year after planting averaged 1285 trees/ha. Additional details of each site can be found in Miller et al. (1995).

In general, a randomized complete block design was used to establish four plots in each of four blocks at each study location. A completely randomized design with four replications was used at Bainbridge and five replications at Pembroke. Treatment plots were approximately 0.1 ha with interior pine measurement plots of approximately 0.04 ha.

Vegetation control treatments included (i) no additional vegetation control following site preparation, (ii) woody control only, (iii) herbaceous control only, and (iv) woody and herbaceous control (total control). Herbicides were applied one or more times each year during the first 3 or 4 years on plots receiving herbaceous control and during the first 3–5 years on plots receiving woody plant control. Treatment of woody vegetation (hardwoods and shrubs) included directed foliar applications of glyphosate or triclopyr in water or basal sprays or wipes of triclopyr in diesel fuel. Control of herbaceous plants typically involved application of sulfometuron in the spring of each year prior to emergence of herbaceous plants. Directed, and often shielded, foliar sprays of glyphosate were applied during the summer as needed to control regrowth of herbaceous plants. Treatments provided excellent control of herbaceous and woody vegetation (Miller et al. 1991, 1995).

Composite samples of foliage were collected from pines on each measurement plot in January following the second and sixth growing seasons. Foliage was collected from the first growth flush of the most recent growing season in the upper one third of the crown. Sample sizes per plot were 90 fascicles at age 2, with five fascicles from each of 18 trees, and 100 fascicles at age 6, with 20 fascicles from each of five trees. Twelve sites were sampled at age 2 and all 13 sites were sampled at age 6. Foliage samples were stored at 4°C until they were oven-dried at 65°C, weighed, and then ground. Foliar N and P concentrations were determined using automated colorimetry on digested 200-mg subsamples. Atomic absorption spectrophotometry was used to determine concentrations of K, Ca, and Mg in the digests. Fascicle nutrient content was obtained by multiplying nutrient concentration, expressed as a proportion of dry mass, by mean fascicle mass. Height and diameter of pines in the interior pine measurement plots were measured during the dormant seasons following the second and sixth growing seasons. Results for groundline diameter at age 2 and diameter at breast height (DBH) at age 6 will be presented.

Individual fascicle mass, nutrient concentration and content, and pine height and diameter from each location and sample date were analyzed using a univariate ANOVA for a  $2 \times 2$  factorial treatment structure in a randomized complete block design. The analysis included tests of the main effects of woody treatment (WT), herbaceous treatment (HT), and their interaction. Because of the large number of study locations and response variables, only a summary of the number of significant positive, significant negative and nonsignificant (neutral) main effects and significant interactions will be presented. Vector analysis was also used to interpret shifts of nutrients with each of the three vegetation control treatments (woody control only, herbaceous control only, and woody and herbaceous control) relative to no treatment (Valentine and Allen 1990; Haase and Rose 1995).

## Results

Herbaceous treatment (HT) and woody treatment (WT) had positive effects on mean pine groundline diameter at all 12 and 9 locations, respectively, at age 2 (Table 2). Positive

Table 1. Description of study sites.

Location	Physiographic Province <sup>a</sup>	Soil Series	Site index (m) <sup>b</sup>	Previous stand	Harvest	Site preparation
Pembroke, Ga.	FCP	Mascotte, Pelham	19.8	6-year-old slash pine burned by wildfire	na <sup>c</sup>	Rebedded (summer 1983)
Atmore, Ala.	MCP	Orangeburg	18.0	Slash pine plantation	Sept. 1983	None, whole-tree chipped at harvest
Bainbridge, Ga.	MCP	Orangeburg, Esto	26.8	Natural mixed pine - hardwood	Winter 1982-1983	KG blade, chop, burn (June 1983)
Jena, La.	MCP	Ruston	22.9	Natural mixed pine - hardwood	Fall 1983	Chop, burn (summer 1983)
Liberty, La.	MCP	Cahaba, Ariel	23.4	Natural mixed pine - hardwood	Apr. 1983	Chop, burn (summer 1983)
Liverpool, La.	MCP	Tangi	19.2	Natural loblolly pine - hardwood	Winter-summer 1983	Chop, burn (summer 1983)
Arcadia, La.	HCP	Sacul	16.8	Natural loblolly pine - hardwood	Fall 1983	Chop, burn (summer 1984)
Counce, Tenn.	HCP	Silerton	17.7	Natural mixed pine - hardwood	Winter 1982-1983	Shear, pile, burn windrows (Aug. 1983)
Tallassee, Ala.	HCP	Cowarts	17.1	Loblolly pine plantation	Apr. 1983	Chop, burn (summer 1983)
Warren, Ark.	HCP	Saffell, Stough	18.9	Natural mixed pine - hardwood	June 1983	Chop, burn (summer 1983)
Appomattox, Va.	PIED	Cecil, Cullen, Iredell	15.2	Natural mixed pine - hardwood	June 1983	Chop, burn (summer 1983)
Camp Hill, Ala.	PIED	Cecil, Pacolet	19.8	Natural mixed pine - hardwood	Spring 1983	Chop, burn (spring 1983)
Monticello, Ga.	PIED	Davidson	24.1	Natural mixed pine - hardwood	Oct. 1982	Chop, burn (summer 1983)

<sup>a</sup>Physiographic province: FCP, flatwoods coastal plain; MCP, middle coastal plain; HCP, hilly coastal plain; PIED, Piedmont.<sup>b</sup>From Miller et al. (1995).<sup>c</sup>Not applicable.

**Table 2.** Summary of loblolly pine height, diameter, individual fascicle mass, and foliar nutrient content and concentration responses to herbaceous and woody treatment ( $p < 0.10$ ).

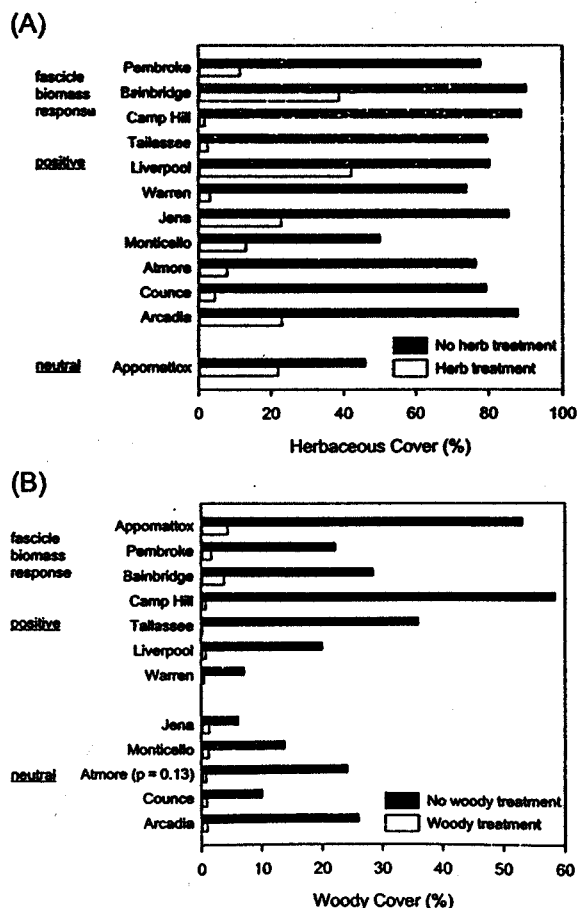
Pine age	Treatment effect and response direction	Height	Diameter	Fascicle mass	Concentration					Content				
					N	P	K	Ca	Mg	N	P	K	Ca	Mg
2	Herbaceous treatment <sup>a</sup>													
	+	9	12	11	6	0	4	0	0	11	10	11	5	3
	0	3	0	1	4	7	7	2	0	1	2	1	6	2
	—	0	0	0	2	5	1	10	12	0	0	0	1	7
	Woody treatment <sup>b</sup>													
	+	3	9	7	4	3	2	0	1	8	6	7	4	3
	0	9	3	5	8	8	10	10	5	4	6	5	7	9
	—	0	0	0	0	1	0	2	6	0	0	0	1	0
	No. significant H × W <sup>c</sup>													
	1	4	2	2	2	2	2	2	2	3	2	2	3	2
6	Herbaceous treatment													
	+	13	12	3	0	3	1	1	1	4	3	2	0	1
	0	0	1	8	12	9	10	10	10	7	9	9	11	10
	—	0	0	2	1	1	2	2	2	2	1	2	2	1
	Woody treatment													
	+	10	12	3	2	1	6	0	0	3	2	6	1	2
	0	3	1	10	10	12	7	7	8	10	11	7	9	11
	—	0	0	0	1	0	0	6	5	0	0	0	3	0
	No. significant H × W													
	3	2	2	2	1	3	1	2	2	3	2	0	0	1

Note: Values are the number of sites that showed a positive (+), negative (-), or neutral (0) response to the treatment.

<sup>a</sup>Test of herbaceous treatment main effect: (herb control + total control)/2 vs. (no control + woody control)/2.

<sup>b</sup>Test of woody treatment main effect: (woody control + total control)/2 vs. (no control + herb control)/2.

<sup>c</sup>Number of sites with significant herbaceous treatment × woody treatment interactions. Test of herb treatment × woody treatment interaction (H × W): (no control + total control)/2 vs. (woody control + herb control)/2.

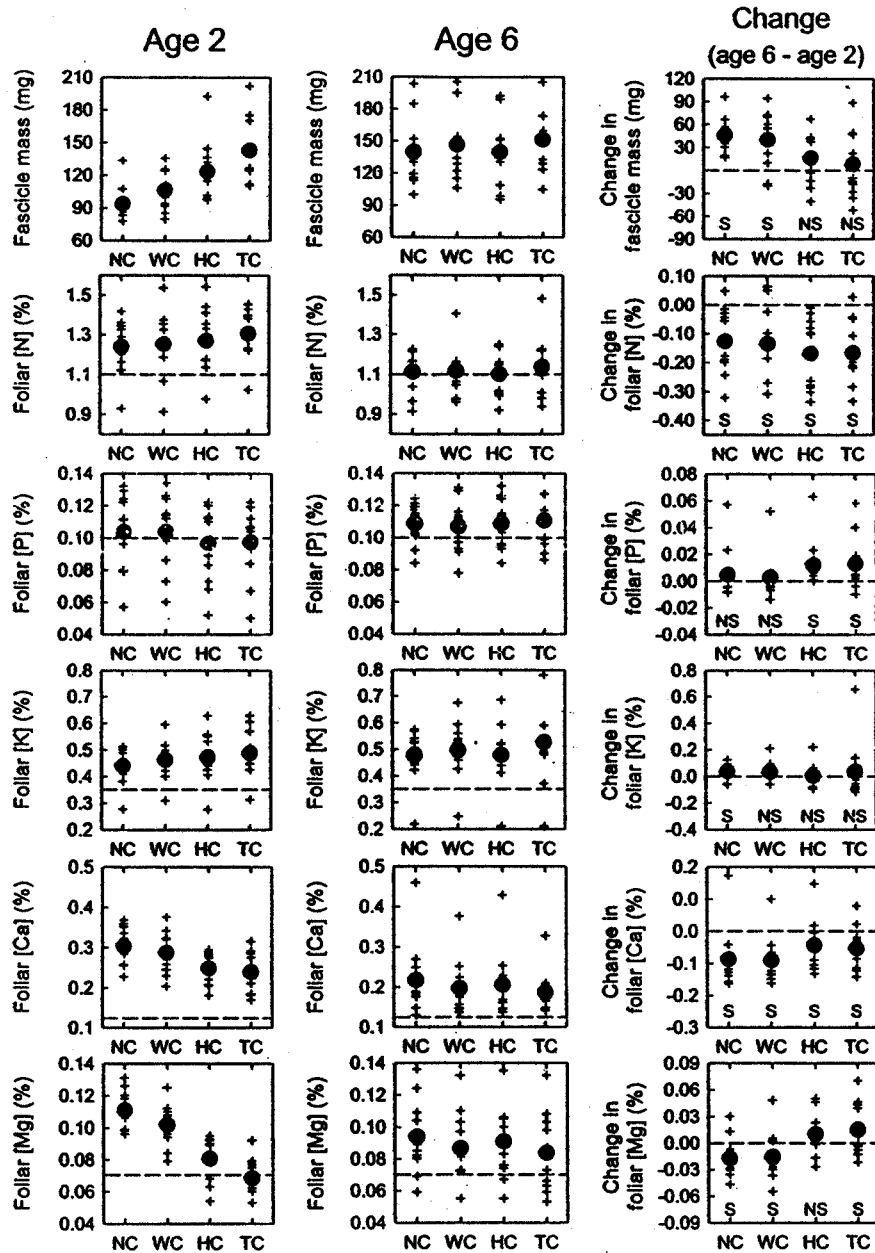


**Fig. 1.** Mean herbaceous cover at the end of the first two growing seasons with and without herbaceous treatment (A) and mean woody cover at the end of the second growing season with and without woody treatment (B) for each location. Locations grouped by direction (positive or neutral) of individual fascicle biomass response to the given treatment.

effects on mean pine height were slightly less frequent, being significant at nine and three locations for HT and WT, respectively. Effects of HT on individual fascicle mass mirrored that for diameter, being significant at 11 of 12 sites. Natural herbaceous cover was low and herbaceous control poor on the nonresponsive site, Appomattox (Fig. 1). At 7 of 12 sites, fascicle mass increased with woody treatment. Other sites were nonresponsive and tended to have lower levels of cover and (or) densities of woody vegetation (Fig. 1). Mean response in fascicle mass across all locations to the four vegetation control treatments ranked as follows: total control > herbaceous control only > woody control only > no control (Fig. 2).

Correlations of plot means for fascicle mass and groundline diameter were significant and positive at all sites, ranging from 0.43 to 0.97 with a median of 0.86. Figure 3 shows the relationship between groundline diameter and individual fascicle mass on two sites in the Middle Coastal Plain that differ in levels of woody vegetation. Under a high level of woody vegetation (Bainbridge), diameter and fascicle mass of seedlings receiving only herbaceous control are more similar to that of seedlings receiving no control or only woody control rather than total control as is the case under

Fig. 2. Individual fascicle mass and foliar nutrient concentration by treatment at pine ages 2 and 6, and the change in values from age 2 to 6. Mean for a location is given by a cross and mean across locations given by a solid circle. Critical values for nutrient concentration as given by Allen (1987) are noted by horizontal broken lines in graphs at age 2 and 6 (NC, no control; WC, woody control only; HC, herbaceous control only; TC, total control (woody + herbaceous control; S, significantly different from zero at  $p = 0.10$ ; NS, not significantly different from zero at  $p = 0.10$ )).



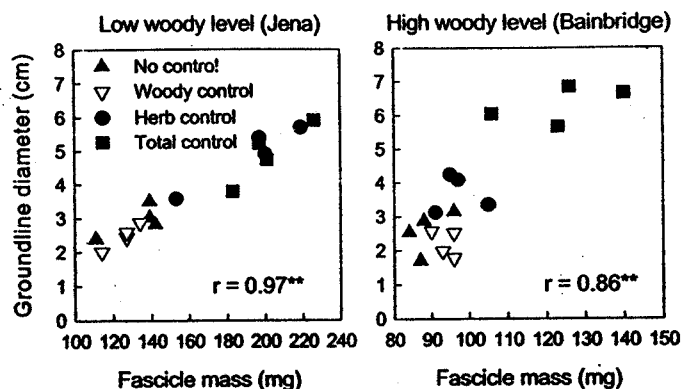
low levels of woody vegetation (Jena). This response pattern at Bainbridge is the source of significant positive HT  $\times$  WT interactions noted for diameter at four locations, all sites with average to above average levels of both woody and herbaceous vegetation (Fig. 1, Atmore, Tallassee, Camp Hill, Bainbridge).

The effect of HT on N, P, and K concentration at age 2 varied by element. Effects of HT on N concentration were positive at half of the sites and neutral at most of the other sites. P concentrations declined (five sites) or were neutral in response (seven sites) to HT. Response in concentration of K was more similar to that for N, increasing on four sites and neutral at all but one of the other sites. Effects of WT on N,

P, and K concentration at age 2 were neutral at two thirds or more of the sites and positive at all but one of the remaining sites. Ranking of treatment means for N and K concentrations across the study sites followed a pattern similar to that for fascicle mass, total control > herbaceous control only > woody control only > no control (Fig. 2), except that differences among treatments were not as pronounced. Frequency of effects of HT and WT on N, P, and K content mirrored that for individual fascicle mass (Table 2).

Effects of HT were generally negative on Ca (10 sites) and Mg (all sites) concentrations at age 2. Woody treatment effects were generally neutral on Ca concentration (10 sites) and neutral (five sites) or negative (six sites) on Mg

Fig. 3. The relationship between groundline diameter and the mass of an individual fascicle at the end of the second growing season for two study locations differing in the level of woody vegetation. Symbols are plot means. \*\*,  $p < 0.01$ .



concentration. Five of the six sites with negative responses in Mg concentration following WT were sites with higher levels of woody vegetation. Ranking of mean Ca and Mg concentrations across the locations was opposite that for fascicle mass, N concentration, and K concentration, namely no control > woody control only > herbaceous control only > total control (Fig. 2). Foliar content of Ca in response to either HT or WT and Mg to WT was positive at about 25% of the sites and neutral for Mg at all or all but one of the other sites for Ca. In contrast, Mg content was negative in response to HT at the other half of the sites.

Vector diagrams of foliar responses on the Arcadia location are indicative of common responses observed on many sites (Fig. 4). These diagrams provide a simultaneous view of fascicle mass and nutrient concentration and content as influenced by treatment. Herbaceous treatment (HT), either as herbaceous only or total control, had the strongest effect on foliar response, with a slightly greater effect for total control. The strong positive effect of HT on individual fascicle biomass is seen in the increase in values of relative biomass isoclines (broken lines). Increases in N and K contents are primarily due to increased fascicle mass rather than increases in concentration. Declines in relative foliar P concentration with HT is offset by proportionately greater increases in fascicle mass such that foliar P content increases. Also readily apparent is the negative effect of HT on Ca and Mg concentrations with no significant effect on nutrient content.

By age 6, both height and diameter were positively influenced by HT and WT at more sites compared to age 2 (Table 2). Effects of HT and WT on individual fascicle mass, and nutrient concentration and content became neutral or more neutral across the sites (Table 2, Fig. 2). A notable exception, typically occurring on sites with high levels of woody vegetation, was the positive response in K concentration or content and negative response in Ca and Mg concentrations with WT.

Mean individual fascicle mass across the sites increased on no control (NC) and woody control only (WC) treatments from age 2 to 6 to become similar to that on the herbaceous control only (HC) and total control treatments (TC) (Fig. 2). Mean N concentration across the sites over the same period

significantly decreased on all four treatments. Age-2 mean N concentration for all treatments was over 1.1% (critical value for N; Allen 1987) at all but one site, averaging 1.27% across the sites. However, N concentration by age six differed little by treatment (range 1.10–1.14%) and averaged 1.12% across the sites.

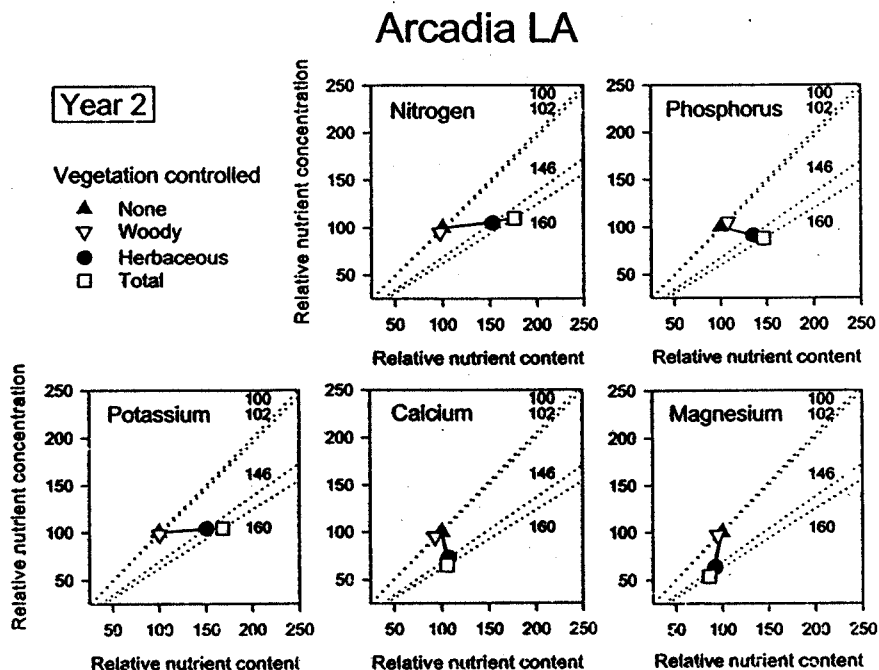
Mean P concentration across the sites significantly increased on plots receiving herbaceous treatments (HC, TC) and was unchanged on the other treatments from age 2 to 6 (Fig. 2). No significant change was noted in mean K concentration for HT or WT over the 4-year period regardless of the treatment. Ca concentration, like N concentration, significantly decreased on average across the sites from age 2 (mean 0.27%) to age 6 (mean 0.20%) on all four treatments. Mean Mg concentration across the sites became more uniform among the treatments by age 6 (mean 0.09%), having decreased on no control and woody control only treatments and significantly increased on herbaceous control only and total control treatments.

## Discussion

Individual fascicle mass and foliar content of N, P and K of seedling loblolly pine were increased during the first 2 years after planting when competing vegetation was significantly reduced. At age 2, the frequency of occurrence of significant, positive effects of vegetation control on fascicle N, P, and K content was comparable with the frequency of effects on seedling diameter across the study locations. Concentrations of foliar nutrients were less influenced overall than content, except increased N concentrations occurred on half of the sites with HT. Increases in seedling foliar N concentration in response to herbaceous weed control have also been observed in radiata pine (*Pinus radiata* D. Don) (Smethurst and Nambiar 1989) and in loblolly pine on deep sandy soils in eastern Texas (Messina 1991). Increases in N concentration have been observed also for loblolly pine seedlings growing in the absence of some, but not all, species of herbaceous weeds in Alabama (Morris et al. 1993). Negative responses in N concentration to herbaceous treatment noted at two locations in this study have been noted in 3-year-old loblolly pine in Virginia (Fredricksen et al. 1993).

Increases in foliar N concentration and content at age 2 may be due to greater availability in soil N resulting from increases in microbial activity and nitrogen mineralization and (or) reduced competition. Reductions in vegetation can result in higher soil temperatures (Nusser and Wentworth 1987) and greater soil water content (Zutter et al. 1986a; Smethurst and Nambiar 1989; Morris et al. 1993), conditions more favorable for mineralization. Nusser and Wentworth (1987) noted soil nitrate and soil ammonium to be negatively correlated with the volume of competing vegetation in a newly planted loblolly pine stand on a clayey-kaolinitic soil in the North Carolina Piedmont. Smethurst and Nambiar (1989) found mineralized soil N to be at least doubled in weed-free areas of a podzolized sandy soil during the first growing season after planting radiata pine. They attributed this difference to a significant uptake of N by weeds since rates of net N mineralization were similar in the presence and absence of weeds.

Fig. 4. Foliar responses to vegetation control at the Arcadia location. Broken lines are isoclines for relative individual fascicle biomass (mg). Concentration, content, and biomass values are relative to the no control treatment.



Declines at age 2 in concentrations of N, P, and Ca with herbaceous treatment and Mg with herbaceous and woody treatment are likely a result of rapid increases in tree crown biomass. Increases in aboveground and whole-crown biomass were previously noted at the Tallassee and Atmore locations at age 1 (Zutter et al. 1986b) and Tallassee at age 4 (Britt et al. 1990). Similar responses in aboveground and whole-crown biomass were likely observed at the other locations because of the high correlation between foliage biomass and (or) leaf area and volume growth (Colbert et al. 1990; Allen et al. 1992).

Several factors may explain diminished positive foliar responses to vegetation control by age 6. By age 4 or 5 there are substantial increases in tree stand biomass resulting from vegetation control (Britt et al. 1990; Allen et al. 1991; Colbert et al. 1990; Dalla-Tea and Jokela 1991) and associated greater use of resources by the developing stands. For example, weed control resulted in lower water stress at age 1, but the effect was absent by the fourth growing season at the Tallassee location (Miller et al. 1987; Green et al. 1991). Vegetation control results in more rapid development of the pine canopy, which shades the developing forest floor and moderates soil temperatures. This may decrease microbial activity and nitrogen mineralization. Net nitrogen mineralization rates in the upper 15 cm of soil have been noted to decline from age 1 to 5 in a loblolly pine stand on a clayey-kaolinitic soil in the North Carolina Piedmont (Vitousek and Matson 1984, 1985; Vitousek et al. 1992) and from ages 1 through 3 in radiata pine stand on a podzolized sandy soil (Smethurst and Nambiar 1995). Forest floor development results in immobilization of N as noted at age 8 at the Tallassee location (Lockaby et al. 1995). Lower concentrations of Ca and Mg with control of woody vegetation on sites with higher levels of hardwood at pine age 6 might be explained in part by the large increases in crown foliage

mass in response to woody plant control and a resultant dilution in concentration of these elements. However, concentrations of both Ca and Mg were above those believed to be important for adequate growth of loblolly pine (Allen 1987). Another possible explanation for these differences may be related to greater cycling of Ca and Mg by deciduous hardwoods compared with conifers (Cole and Rapp 1981) and, thus, possibly greater soil availability of these elements in the absence of woody control.

## Conclusions

This regionwide study having uniform, replicated procedures has provided a broad first look at foliar nutrition of young loblolly pine plantations receiving intensive woody and (or) herbaceous plant control. Intensive vegetation control strongly influences pine growth, including foliar mass and nutrient status. Effects of vegetation control on fascicle mass and nutrient concentration and content were most pronounced at age 2, with control of herbaceous plants typically having significant effects at a greater number of locations than that observed for control of woody plants. The increase in foliar concentration of N with herbaceous plant control at half of the study locations is of particular significance since additional N will be available for internal transfer and use in plant growth once the growing season begins. Fascicle mass at age 2 was strongly correlated with groundline diameter and may provide an indication of pine growth in very young stands. Differences in fascicle mass and nutrient status among vegetation control treatments were minimal by age 6. The lack of positive effects from woody or herbaceous control at age 6 is attributed in part to the greater nutrient demands by the larger crop pines and associated woody and herbaceous competitors. Immobilization of nutrients in the litter and decreased mineralization rates associated with

forest floor and stand development may be contributing to lower availability of nutrients.

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